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HOMOPLASY AS A LAW OF LATENT OR POTENTIAL HOMOLOGY.

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My study of teeth in a great many phyla of Mammalia in past times has convinced me that there are fundamental predispositions to vary in certain directions; that the evolution of the teeth is marked out beforehand by hereditary influences which extend back hundreds of thousands of years. These predispositions are aroused under certain exciting causes and the progress of tooth development takes a certain form converting into actuality what has hitherto been potentiality.

Science, N.S., Vol. VI, No. 146 (Oct. 15, 1897), pp. 583–587.

In previous communications, as shown in the above quotation, I have spoken of the "potential of similar variation," as covering cases of the independent evolution of identical structures in the teeth of different families of mammals, especially in relation to the homologous "antecrochet" and "crochet" folds in the teeth of horses, rhinoceroses, and we may now add, of titanotheres (Osborn, '94, p. 208). In the present communication I propose to treat somewhat more fully of the same phenomenon, as a special form of homology which has been clearly defined by Lankester in 1874 as *homoplasy*, but into which paleontology has brought the idea of "potential."

THE BROAD SIGNIFICANCE OF ANALOGY.

We are familiar with the classic distinction of analogous organs as having a similarity of function: *analogy* (Owen, **'43**, p. 374), "a part or organ in one animal which has the same function as another part or organ in a different animal"; Lankester (**'70**): "Any two organs having the same function are analogous, whether closely resembling each other in their structure and relation to other parts or not; and it is well to retain the word in that wide sense." Analogous organs may or may not be homologous. "Analogy" is therefore an extremely broad and comprehensive term, and it appears that we must include under it all cases of the similar evolution of organs either of common or of different origin due to similarity of function. For example, the "analogous variation" of Darwin, the "homoplasy" of Lankester in part at least, the "convergenz" of German writers, the "homomorphy" of Fürbringer, the "heterology," "parallels," and "parallelism" of Hyatt, of Cope (**'68**, also *Origin of the Fittest*, p. 96), of Scott, and of most American writers, are all illustrations of analogy and may be very misleading as to homology.

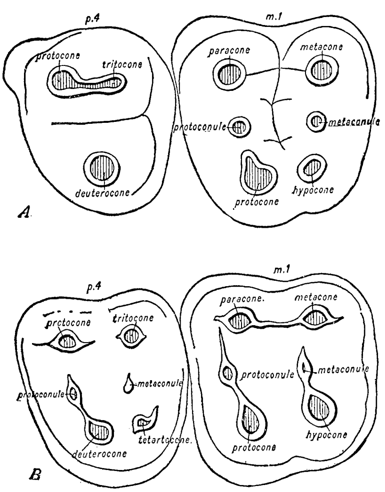

FIG. 1.— Fourth upper premolar and first molar of primitive ungulates. *A*, Euprotogonia; *B*, Hyracotherium. Not believed to be genetically related, yet exhibiting independent or homoplastic evolution of homologous cusps.

As Scott observed in 1896, "Parallelism[1] and convergence of development are much more general and important modes

[1] The term "parallelism" was employed by Cope in his essay of 1868 on the "Origin of Genera" (reprinted in the *Origin of the Fittest*) in two quite different senses: first, in relation to recapitulation in ontogeny, — "Those which accomplish less [stages] are *parallel* with the young of those which accomplish more [stages]; second, quite in the modern sense (*op. cit.*, pp. 96–104) of independently acquired resemblances in different groups. As employed by Scott in his essay

of evolution than is commonly supposed. By parallelism is meant the independent acquisition of similar structure in forms [*i.e.*, animals] which are themselves nearly related, and by convergence such acquisition in forms [*i.e.*, animals] which are not closely related, and thus in one or more respects come to be more nearly alike than were their ancestors."

The term "homoplasy" (Lankester) has been long used by the writer and others in a somewhat similar sense, but it is not equivalent either to "parallelism" or "convergence." As will be seen below, the fundamental idea is different, because homoplasy always involves homology, while parallelism and convergence may or may not involve homology.

ANALOGY IN EVOLUTION.

ANALOGY.

- *Analogous Variation* (Darwin). Similar congenital variation in more or less distantly related animals and plants.
- *Parallelism.* Independent similar development of related animals, plants, and organs.
- *Convergence.* Independent similar development of unrelated animals, bringing them apparently closer together.
- *Homoplasy* (Lankester) (?*Homomorphy*, Fürbringer). Independent similar development of homologous organs or regions giving rise to similar new parts.

In brief, analogy embraces similar changes due to similar adaptation in function both in homologous and in non-homologous organs, both in related and in unrelated animals.

THE LIMITED SIGNIFICANCE OF HOMOLOGY.

Owen ('**43**, p. 379), Lankester ('**70**), and Fürbringer have especially defined and elaborated the very ancient conception of homology, as employed by Oken, Geoffroy St. Hilaire, and Vicq d'Azyr : *homology* (Owen, '**43**), "the same organ in

"On the Mode of Evolution in the Mammalia" ('**91**, pp. 363–367), "parallelism" is used in a very broad sense as affecting the skeleton and teeth, on the principle "that identical modifications of structure, constituting evolution of types, have supervened on distinct lines of descent," as embracing not only single characters but whole series of them.

different animals under every variety of form and function"; *homogeny* (Lankester, '70): "Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called *homogenous*." E. B. Wilson ('95, pp. 101–124) has shown that the comparative anatomical test of homology is more reliable than the embryological. Gegenbaur ('98, pp. 23–25) has given a full presentation of the distinctions as the basis of comparative anatomy; in his recent great work ('98, p. 23) he presents the matter in terms which may be briefly analyzed with the usages of other authors, as follows:

I. HOMOLOGY, GENERAL: as of vertebræ and limbs.

1. HOMOTYPY: as of opposite limbs, eyes, kidneys, etc.
2. HOMODYNAMY: (in part the "general," in part the "serial," homology of Owen; the "meristic" homology of Bateson). Corresponding limbs, parts, segments (*e.g.*, the humerus and femur) on the same side of the body.
3. HOMONOMY: parts which are in the same transverse axis of the body, or on only one section of the longitudinal axis; *e.g.*, the rays of the fins of fishes, the single fingers and toes of the higher vertebrates are homonomous organs.

II. HOMOLOGY, SPECIAL: (the "homogeny" of Lankester).

1. COMPLETE HOMOLOGY of elements which have retained their relations unchanged, as of single bones from the Amphibia to the Mammalia.
2. INCOMPLETE HOMOLOGY, as of organs which have either gained new parts or lost certain of their parts.
   a. *defective*, as in comparison of fins of teleosts and of selachians.
   b. *augmentative*, as in the heart of cyclostomes and of the higher vertebrates.
   c. *imitative*, as where different vertebræ connect with the ilium and become sacral.

III. HOMOMORPHY (Fürbringer): from these homologies certain structures are to be distinguished as *homomorphic* which are more or less similar to each other but stand in no phylogenetic connection.[1]

Homomorphy comes nearest, as we understand it, to the "homoplasy" of Lankester, but the latter term has the priority of definition.

[1] Literally translated from Gegenbaur.

Distinction between Homogenous and Homoplastic Organs.

In the strictest sense, special or genetic homology, the "homogeny" of Lankester, is the only absolute homology. For example, in all four-limbed vertebrates, or Tetrapoda (Credner), the first and second phalanges of the tibial digit or hallux are homogenous; the earliest tetrapods had such phalanges, so far as we can judge from both paleontology and embryology, and all others are derivatives.

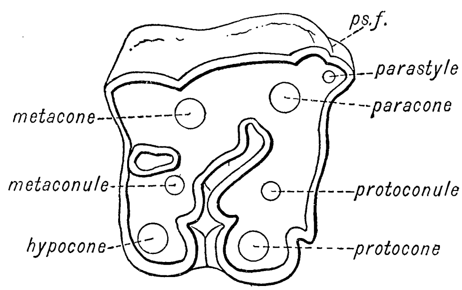

Fig. 2. — Ideal embryonic ground plan of rhinoceros molar, showing relation of primitive cusps to the folds and crests.

But suppose we should discover that these two phalanges had originated independently in several different classes of vertebrates, and were not derivatives; should they then be considered analogous or homologous? "Again," says Lankester ('70), "it may perhaps be admitted that the common ancestors of the Osseous Fishes and Mammalia had a skull of decidedly undifferentiated character, with a much less amount of differentiation than is observed in the skulls of either of these groups. It is only in so far as they have parts represented in the common ancestor that we can trace *homogeny* in these groups; and yet the *homology* of a vast number of bones in the skull of the two is discussed and pointed out." Suppose, accordingly, that in the formation of dermal roofing bones in different orders of fishes a pair of bones corresponding in position to the parietals should arise

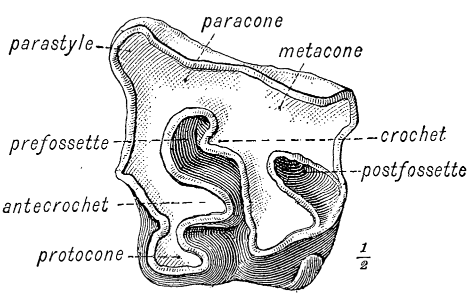

Fig. 3. — Molar tooth of an Upper Miocene rhinoceros (Teleoceras), showing origin of secondary folds.

independently, or that in the evolution of the teeth cusps should arise independently having the same form and position, — what criterion should be applied? All such structures are habitually regarded as homologous, yet it is apparent that they are not derivatives of each other and therefore not homogenous or homologous in the strictest sense.

Such cases of independent evolution of apparently homologous organs I recently proposed[1] to signify as *potential,* or *latent homology,* borrowing the term "latent" from Galton as indicative of a germinal rather than of a patent or adult character, and the physical term "potential" as expressing the innate power or capacity to develop a certain organ. But my colleague, Prof. Edmund B. Wilson, pointed out to me that such cases were almost exactly covered by the *original definition* of the word "homoplasy" by Lankester (**'70**, p. 42), as shown in the subjoined quotations from his essay:

> When identical or nearly similar forces, or environments, act on two or more parts of an organism which are exactly or nearly alike, the resulting *modifications*[2] of the various parts will be exactly or nearly alike. Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts in the two organisms will be nearly or exactly alike. I propose to call this kind of agreement *homoplastic* or *homoplasy.*[3] . . . What is put forward here is this: that under the term "homology," belonging to another philosophy, evolutionists have described and do describe two kinds of agreement, — the one, now proposed to be called "homogeny," depending simply on the inheritance of a common part; the other, proposed to be called "homoplasy," depending on a common action of evoking causes or moulding environment on such homogenous parts, or on parts which for other reasons offer a likeness of material to begin with.

$$\text{Homology thus includes} \begin{cases} \text{Homoplasy.} \\ \text{Homogeny.} \end{cases}$$

It follows that subsequent writers, including myself, have misused the term "homoplasy," confusing it with "parallelism"

[1] In a communication before the National Academy of Science, Nov. 13, 1901.

[2] Italics are mine.

[3] At this time Lankester accepted Herbert Spencer's Lamarckian views. Subsequently he abandoned the mechanical inheritance theory for the pure natural selection theory.

and "convergence," which, as we have seen, may affect absolutely non-homologous structures. *Homoplasy should be confined to structures in which there is an element of homology.*

Independently of Lankester (that is, not familiar with his paper) I had therefore reached a similar conclusion through years of observation in paleontology. I would now like to expand an idea which he also lightly suggested in 1870 in the words, "*or on parts which for other reasons show a likeness of material to begin with.*"

The Law of Homoplasy as in Part Identical with Definite or Determinate Variation.

As observed in the evolution of the teeth especially, homoplasy appears to be of very great importance, not on the technical grounds of uniformity in nomenclature, but because it seems to coincide with the principle of definite or determinate evolution, a principle which may be of wider application.[1]

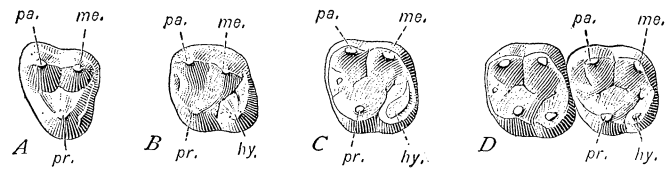

Fig. 4. — Superior molars of primates, Anaptomorphus to Homo, showing independent or homoplastic origin of the hypocone, *hy*, from the cingulum.

From the time of the "Origin of Species" it has been admitted that evolution, so far as it depends upon variation, is not in every possible direction, but is limited to certain changes, the expression of certain hereditary or constitutional causes which we do not in the least understand. The evolution of the teeth of mammals enabled me in 1889 to give many concrete illustrations of this principle and to show that variation is hardly the proper term to apply to rudiments which do not arise in a variable but in a fixed manner.

[1] See especially the correspondence of Darwin and Asa Gray; also Osborn, The Palæontological Evidence for the Transmission of Acquired Characters, *Nature*, Jan. 9, 1890; the Orthogenesis and Orthoplasy of Eimer, Lloyd Morgan and Baldwin; Baldwin's *Dictionary of Philosophy and Psychology*, vol. i, p. 243.

It appears that von Waagen suggested the term "mutation" for immeasurable variations somewhat similar to these. Scott in 1891 (**'91**, p. 388) pursued the idea further in the following striking passage: "These facts at least suggest the possibility that individual variations are not incipient species, but that the

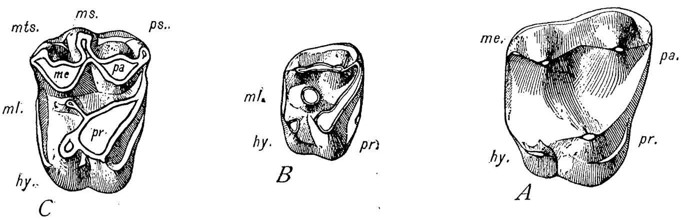

FIG. 5.—Superior molars of primates. *A*, Adapis; *B*, Hyopsodus; *C*, Notharctus. Showing homoplastic cusps, *hy*, *ml*, *ps*, *ms*, *mts*.

causes of transformation lie deeper, and act with more or less uniformity upon large numbers of individuals. It may, perhaps, be the outcome of future investigations, that while variations are generally due to the union of changing hereditary tendencies, mutations are the effect of dynamical agencies operating long in a uniform way, and the results controlled by natural selection. While this *may* be true, a great many facts must be gathered in its support, before it can be regarded as more than a suggestion." Scott subsequently, in his article "Variations and Mutations," expanded this idea: "Bateson's results, as compared with those of paleontology, confirm this distinction in many significant ways and emphasize strongly the difference between variation and that steady advance along definite lines which Waagen called mutation." This paper in turn is said to have influenced de Vries's recent work, *Die Mutationstheorie.*

It is a singular coincidence that the human teeth were selected by both Empedocles and Aristotle to test the "survival of the fittest" *versus* the purposive or teleological theory of evolution. I pointed out in the papers above referred to (Osborn, **'89**, pp. 561–566; **'90**) the significant fact that new cusps of the molar teeth do not appear at random, but at certain definite points; that they are at first so minute that

they can barely be perceived, so that it is difficult to theoretically assign them a survival value in the struggle for existence; that the mechanical or Lamarckian explanation is the only one which can be offered[1]; I laid the chief stress, however, not upon the mechanical explanation, but upon definite or determinate origin, and this has been confirmed by the subsequent study of thousands of teeth in different families of mammals. The still more significant fact that this definite and determinate evolution was proceeding independently in a great many different families of mammals did not at the time impress itself so strongly upon my mind.

If molar teeth are found independently evolving in exactly similar ways in such remote parts of the world as Switzerland, Wyoming, and Patagonia, it is obvious that the process is not governed by chance but represents the operation of some similar or uniform law deduced from the four following considerations:

Firstly, the teeth differ from all the other tissues and organs of the body in being preformed, beneath the gum.[2] Unlike all other organs they are not modified, improved, or rendered more adaptive by use; on the contrary, after the first stage of wear,

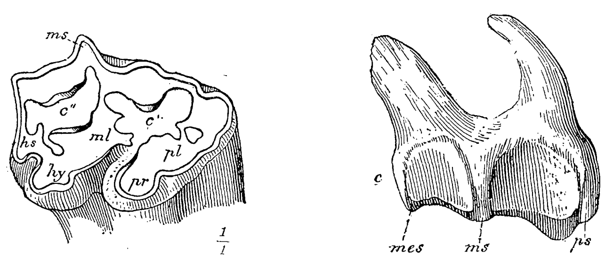

FIG. 6. — Superior molar of Merychippus, showing styles *ps*, *ms*, *mts*, and conules *pl*, *ml*, homoplastic with those of the wholly unrelated primate molar, Fig. 5, *C*.

the longer they are used the more useless and less adaptive they become. Thus, new structures in the teeth do not first appear as *modifications* (as distinguished from congenital

[1] Ryder and Cope confidently advanced the mechanical explanation; it is not without grave difficulties, owing to the lack of an heredity theory.

[2] The importance of this fact was first pointed out to me by Prof. E. B. Poulton of Oxford.

variations) in course of life, as is so often if not invariably the case with new structures in the skeleton. New cusps, folds, crests, and styles are invariably congenital. Thus, of all organs of the body the teeth most exclusively and purely represent the current of stirp, germinal, or constitutional evolution.

Secondly, the teeth are, nevertheless, among the most progressive organs in the body. Whereas the adaptation of the skeleton, among the mammals at least, is by a constant loss or numerical reduction of parts, the adaptation of the teeth is by a constant addition and modeling of parts (Osborn, '88, pp. 1067–1079).

Thirdly, according to the present paleontological evidence many of the different families and orders of mammals diverged from each other at a time when they possessed three cusps on the upper molar teeth and from three to five cusps on the lower molar teeth. This being the case, only the cusps comparable in different orders of mammals with these original three upper and five lower cusps are derivatives or homogenous.

Fourthly, it follows that the new cusps of the teeth furnish an example of homoplasy independent of the individual modification.

Thus, we may say that in the teeth at least *homoplasy involves a law of latent or potential homology*, without professing to understand what is its significance.

We should, *a priori*, expect that if additional cusps were added independently in different families and orders of mammals in different parts of the world, under highly different conditions, the teeth of the higher Mammalia would present very great diversity. As a matter of fact, the new cusps in different families are absolutely uniform up to a certain limit.[1] In the twenty-three orders of placentals and in the seven marsupial families, many of which are adaptively equivalent to orders, the independently developed fourth to eleventh cusps of the upper molars, if so many are developed, are uniform and may be termed homologous; the eight cusps and folds succeeding the original homogenous three arising, if at all,

[1] The excess of this limit is in multituberculism, or polybunodonty, where cuspules are indefinitely multiplied.

at similar points and presenting a latent homology or homoplasy. The record in the upper molar teeth stands thus :

HOMOLOGY.

HOMOGENY	HOMOPLASY
Primitive three cusps common to all mammals.	Cusps or folds which are or may be independently developed in different orders.
Protocone	Hypocone
Paracone	Metaconule
Metacone	Protoconule
—	Parastyle
—	Mesostyle
—	Metastyle
—	Protostyle
—	Hypostyle

This expresses the comparison of mammals as a whole. Within many of the orders, such as the Perissodactyla, which arise from six cusped ancestors, the homology is different.

HOMOLOGY.

HOMOGENY	HOMOPLASY
Protocone	Parastyle
Paracone	Mesostyle
Metacone	Crista
Hypocone	Crochet
Protoconule	Antecrochet, etc.
Metaconule	—

The elements to which these terms are applied are best exemplified in the molar teeth of some of the primitive horses (Fig. 6).

The teeth are by no means the only structures which evolve under this principle, the skull, vertebral column, and limbs also evolving under it more or less completely; but the teeth afford a singularly beautiful illustration of it because they exclude individual modification.

The chief object of this communication is to enforce the recognition of homoplasy as something which must be accounted for. These homoplastic cusps do not arise from selection out of fortuitous variations, because they develop directly and are not picked from a number of alternates. Neither does it appear that the mechanical-inheritance theory, if granted, would produce such a remarkable uniformity of result. We are forced to the conclusion that in the original tritubercular constitution of the teeth there is some principle which unifies the subsequent variation and evolution up to a certain point. Herein lies the appropriateness of Lankester's phrase, "a likeness of material to begin with."

Philosophically, predeterminate variation and evolution brings us upon dangerous ground. If all that is evolved in the Tertiary molar tooth is included in a latent or potential form, in the Cretaceous molar tooth we are nearing the *emboîtement* hypothesis of Bonnet or the archetype of Oken and Owen. Embryologists have recently gotten into the same dilemma, and my colleague, Wilson, has proposed to drop the idea "homology" altogether and substitute the idea "equivalent." In the present case, however, I think we have to deal with homology or, more strictly, with a *principle intermediate between homology and analogy*.

In a paper recently read before the American Morphological Society (December, 1901), this author has urged the necessity of adhering as closely as possible to the historical standard in the embryological study of homology, and of avoiding the use of the term "homology" when this standard is not available. He therefore suggests for descriptive purposes the use of the noncommittal terms "equivalent" and "homoblastic," the former being applied to embryonic structures of like fate (*i.e.*, giving rise to homologous parts), the latter to those of like embryonic origin. The only decisive test of the homology is historic community of derivation (*i.e.*, homogeny).

BIBLIOGRAPHY.

'68 COPE, E. D. On the Origin of Genera. *Proc. Acad. Nat. Sci. Phila.* October, 1868.

'87 COPE, E. D. The Origin of the Fittest. 8vo. New York.

'98 GEGENBAUR, CARL. Vergleichende Anatomie der Wirbelthiere. 8vo. Leipzig, 1898.

'70 LANKESTER, E. R. On the Use of the Term "Homology" in Modern Zoölogy and the Distinction between Homogenetic and Homoplastic Agreements. *Ann. Mag. Nat. Hist.* Ser. 4, vol. iv, pp. 34–43.

'89 NEUMAYR, M. Die Stämme des Thierreiches. 4to. Pp. 60–61. Vienna, 1889.

'88 OSBORN, HENRY F. The Evolution of Mammalian Molars to and from the Tritubercular Type. *Amer. Nat.* Vol. xxii (December, 1888), pp. 1067–1079.

'89 OSBORN, HENRY F. The Palæontological Evidence for the Transmission of Acquired Characters. *Amer. Nat.* Vol. xxiii (1889), pp. 561–566.

'90 OSBORN, HENRY F. Evolution and Heredity. *Biological Lectures, 1890, Marine Biological Laboratory, Woods Hole.*

'94 OSBORN, HENRY F. The Rise of the Mammalia in North America. *Proc. Amer. Assoc. Adv. Sci.* Vol. xlii (1893), pp. 187–227.

'43 OWEN, RICHARD. Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals, delivered at the Royal College of Surgeons in 1843. 8vo. London, 1843.

'91 SCOTT, W. B. On Some of the Factors in the Evolution of the Mammalia. On the Osteology of Mesohippus and Leptomeryx, with Observations on the Modes and Factors of Evolution in the Mammalia. *Journ. of Morph.* Vol. v, No. 3 (1891), pp. 379–402.

'94 SCOTT, W. B. On Variations and Mutations. *Amer. Journ. Sci.* Vol. xlviii (November, 1894), pp. 355–374.

'96 SCOTT, W. B. Palæontology as a Morphological Discipline. *Biological Lectures, 1895, Marine Biological Laboratory, Woods Hole.* Pp. 43–61. Boston, 1896.

'01 DE VRIES, HUGO. Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich. 8vo. Leipzig, 1902.

'95 WILSON, E. B. The Embryological Criterion of Homology. *Biological Lectures, 1895, Marine Biological Laboratory, Woods Hole.* Pp. 101–124. Boston, 1895.